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PUPAL SOUND PRODUCTION OF SOME LYCAENIDAE

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STRUCTURE AND SOUND

Introduction

SOUNDS PRODUCED BY PUPAE have been known for nearly 200 years (Kleeman's listening to *Callophrys rubi* L., 1774). Prell (1913) described the noise and made drawings of the stridulatory devices in *Thecla quercus* L. Hinton (1948) summarized the general literature on pupal sound in the Lepidoptera and presented four types of mechanisms involved. Downey (1966) brought together the scattered information on sound in pupae of Lycaenidae and noted the occurrence of the organs which produce sound in a great number of species, and he was able to increase the list of known sound producing Lycaenid pupae from 25 previously reported to 82.

The external structures involved in sound production in Lycaenidae can be located to membrane 4 (i.e. the membrane infolded between segments 4 and 5), but is always found, if present, on membrane 5, and generally limited to the dorsal region. An anterior stridulating plate is found, often heavily sclerotized and variously sculptured; then follows a thin transparent membrane devoid of common structural features; posteriorly a file, opposed to the plate, completes the device.

Prell (1913), Strawn (1964) and Downey (1966) have described longitudinal muscles in various Lycaenids, connecting parts on either side of the stridulating apparatus, both in pupae and in the pharate adult inside the pupa; in the latter the muscle continues in a short ligament from the integument to the fifth intersegmental membrane of the pupa; Strawn calls these "stridulating attachments." The presence of this muscle (and later muscle + ligament) explains, how the pupa through-

out is able to produce sounds from early pupal stage until emergence. It was not possible to locate scars or rudiments of the ligament on imagines. Antagonistically working muscles were not found, and it is therefore assumed that the fluid pressure may return the movement to a resting position.

In *Lycaena thoe* Guer. Downey (1966) detected a pupal sound within minutes after the larval skin was shed, and an individual was also heard to stridulate up to the emergence.

There is some question as to which stage of the life cycle is involved in this phenomenon. The name "pharate" has been proposed by Hinton (1946) to designate the phase of an instar which is enclosed within the cuticle of the previous instar, and Downey holds that stridulating response in Lycaenidae may be limited to pharate adult behaviour, which accordingly implies that the real pupal stage would have to be considered as occurring during that brief quiescent period ordinarily thought of as "pre-pupal" interval, and most "pupal" movements as belonging to the pharate adult.

Downey (1966) working with *Lycaena thoe* Guer., was able to associate the sound with "extremely rapid movements" of abdominal segments posterior to segment five, and here he disclosed the microscopic stridulatory organs. Dickson (1952) stated that when a pupa of *Phasis zeuco zeuco* L. was touched, the portion of the abdomen beyond the fourth segment was seen to move with a "rapid, almost trembling motion."

PRESENT INVESTIGATIONS

In view of this work and the many theories raised to explain the function of the sounds produced, it is remarkable that so little experimental research on live pupae has actually been done.

The following pages describe a number of varied experiments which have been carried out with pupae of *Aricia artaxerxes* F. (*allous* G.-Hb.)—50 specimens of ssp. *vandalica* Kaaber and Hoegh-Guldberg, and 11 ssp. *salmacis* Stph., 10 *A. agestis* Schiff., 10 *Polyommatus icarus* Rott., 5 *Plebeius argus* L., 2 *Thecla quercus* L., and 18 *Celastrina argiolus* L.

STRUCTURES AND SOUNDS INVESTIGATED IN *Aricia artaxerxes*
AND *A. agestis*

Anatomy

The two *Ariciae* species which were the main subject of the experiments were eminently suited for the purpose, as pupal development at ordinary room temperature is regular and of only about 15 days duration. After two to four days in the pre-pupal stage, the larva casts its skin and the fresh pupa is pale green and soft, and for the first day or two so thin-walled that if it is injured, nearly all the contents will run out in clear drops. It cannot produce sounds until it is 3-4 days old and hardened. (If the newly-formed pupa of *Lycaena thoe* Guer. should in fact be able to produce sounds, the stridulating mechanism must be chitinized even in the larval stage).

There was not found any difference, neither in anatomy nor concerning the sounds, between *A. agestis* and *A. artaxerxes*.

Aricia pupae can produce sounds from the fourth pupal day and from then regularly until emergence ten days later.

In the rigid pupae of the 6 *Lycaenids* investigated, only this cleft between 5th and 6th abdominal segments on the dorsal side allows of any larger movement (Fig. 1).

6' 5' 4' 3' 2' 1' segm.

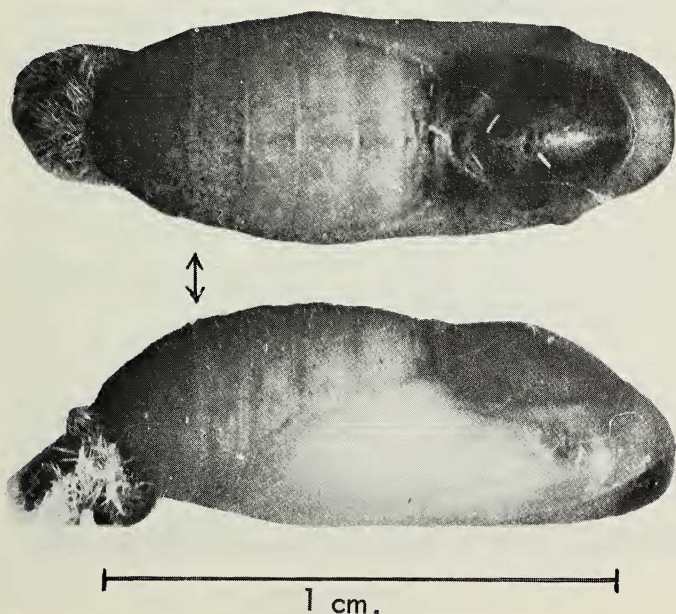


Fig. 1.—Pupa of *Aricia artaxerxes vandalica*, dorsal and lateral view.

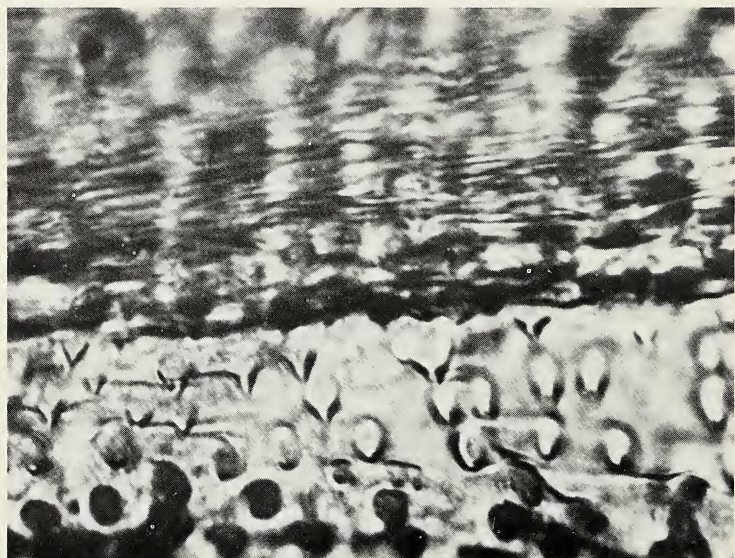
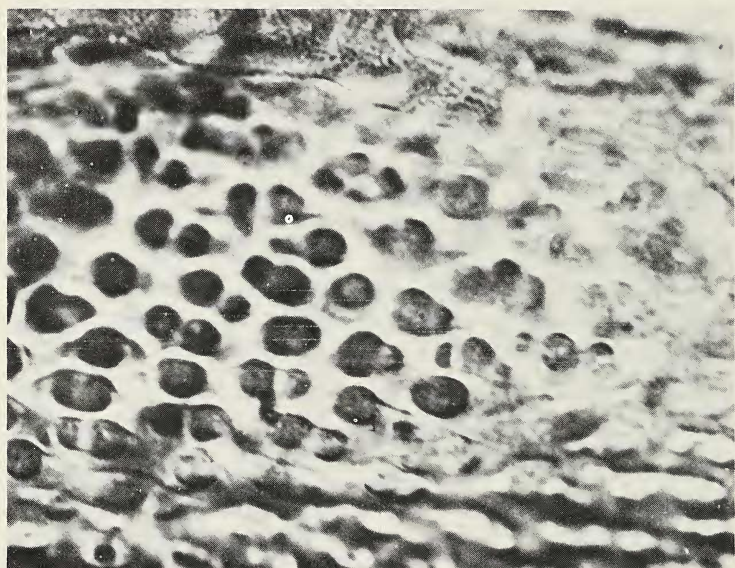


Fig. 2.—Part of stridulating organs of pupa of *Aricia artaxerxes vandolica*.
From left: file, membrane and stridulating plate. Enlarged 400x.

The stridulatory devices in an *Aricia* pupa is seen Fig. 2. The stridulating "plate" in both species is on the anterior part of the intersegmental cleft (on the posterior infold of segment 5). It has a typical grained appearance, resembling very much the creased areas in old shoe leather. This "plate" is not very heavily sclerotized, rather less than the segments, and is defined more by the rough grained texture rather than by its colour. The plate extends laterally only to about the region of the spiracles. In some regions, particularly dorsal, the raised "grains" become elevated and may be defined as rounded tubercles. They are not pointed however, as are the teeth on the posterior inflection (anterior part of segment six). A rather unique feature of both of these species, not found in other Lycaenid genera, is that there is a suggestion of a grained plate and teeth between segments 6/7 as well as 5/6. Often in other species the teeth are present in relatively the same position between several segments, but the *plate* is usually lacking.

Concerning the posterior teeth (which are rubbed across the grained plate to produce the sound): they are of irregular size (some smaller than others) and of indefinite geometric arrangement, even though there is a tendency to occur in oblique alignment (=rows). (Description by Downey, i.l.)

Correspondence between visual and auditory observations

If a pupa was observed with suitable magnification, when sound production took place, it was seen, that there was a movement (an opening and closing of the cleft between segments 5 and 6), corresponding in length to a pulse in the sonagram, and then a short interval, after which the movement was repeated several times, synchronizing with the sound, mostly with a total duration of 300-700 millisec.

The correspondence between visual and auditory observations was very clearly demonstrated, when a videotape through a microscope was used.

In other words, concerning the periodical pulse-trains in these Lycaenids there was no question of "extremely rapid movements" having been observed. If such rapid movements take place, they can only be hidden within the fold, it then being merely the preparatory movement of the file being moved into contact with the plate which could be seen. In my opinion, however, it is the actual movement of the file against the stridulating plate which I was able to observe.

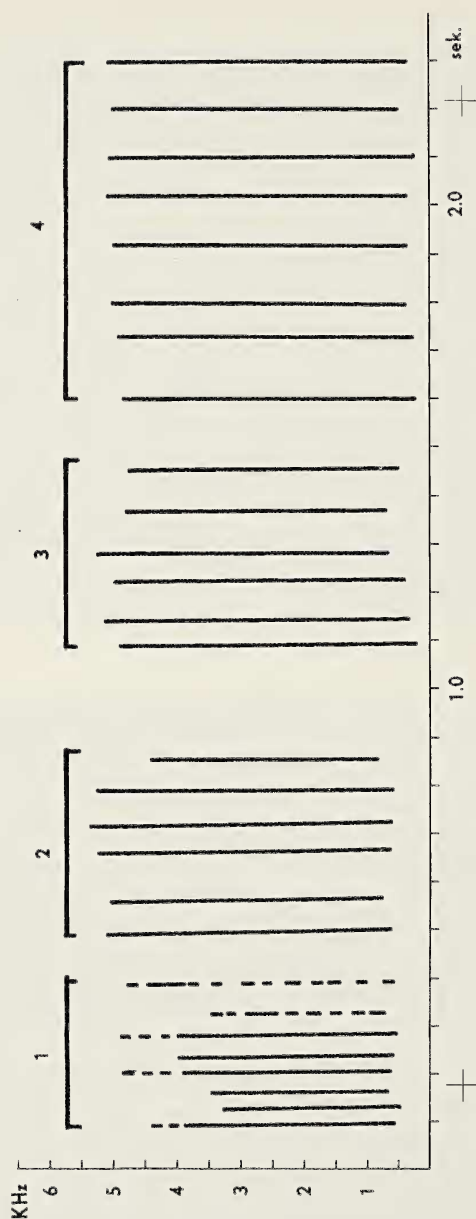


Fig. 3.—Partially schematic sonograms of one pulse-train from 4 different pupae of *Arctia artaxerxes vandatica*.

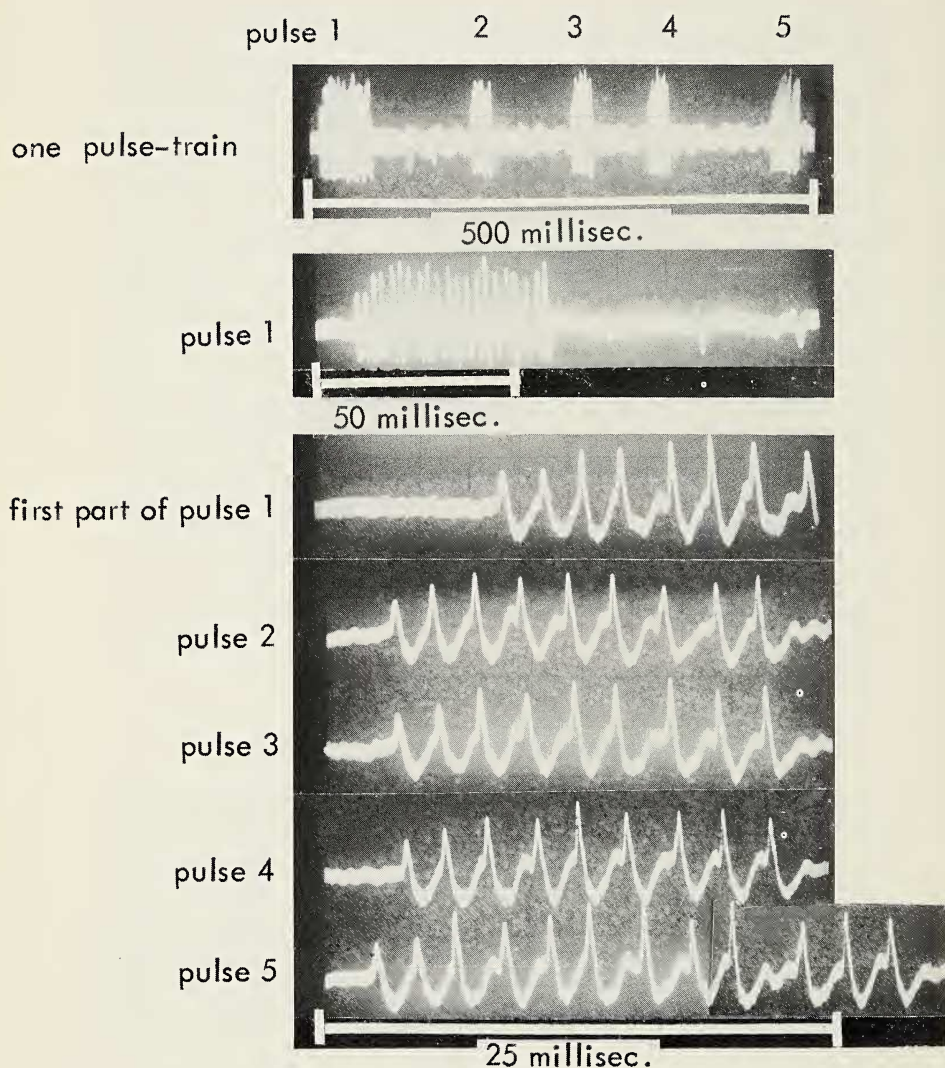
Audiospectrograph analyses

On the basis of a tape recording (NAGRA II BH and Sennheiser microphone) a number of sonagrams have been made from individual *Aricia* pupae that have produced sounds when shaken in a jar or tickled with a brush or a human hair. After a latent period of 700 to 1300 millise. the sonagram showed a series of sounds with a wide uniform frequency spectrum ranging up to 5-6 kHz. The sound consisted of a pulse-train (terminology from Broughton (1963)) of (4) 6-8 (10) pulses, either in rapid succession (intervals of 30 millise.) or with longer intervals (up to 140 millise.) The pulses in the train were seldom regular; usually they appeared in irregular succession and were of slightly varied intensity (Fig. 3). Consequently, the duration of the entire pulse-train varied and might be from 300 to 700 millise. The pulse-train might sometimes occur as part of a short rhythmical period; for instance, having been shaken once, a pupa produced, within a few seconds, 3 pulse-trains each of 8-9 pulses at regular intervals. However, the pauses between such repeated pulse-trains were as a rule of unequal length, for instance 200-350 millise. To judge from the construction of the sound apparatus compared with the sonagrams, it may be assumed that a pulse-train results from the pendulum movements of a plate and a file against each other corresponding to the pulses.

Oscillograph analysis of vibrations

A 10-day-old pupa of *Aricia artaxerxes vandalica* was placed on a gramophone turntable; the lightweight pick-up was balanced further and placed on the back of the pupa, and the numerous vibrations were tape-recorded and then oscillographed. The pupa reacted vigorously with pulse-trains, usually consisting of 5 pulses; the sounds were emitted both as "spontaneous" reactions to the touching of the pick-up, and when the front part of the pupa furthermore was touched with a human hair.

Fig. 4 shows an oscillogram of such a pulse-train. It appears that the wave form of individual pulses are practically identical. This especially applies to the 3 middle pulses which are also of exactly the same length. It may indicate that the same teeth of the file rub across the same irregularities on the stridulation plate.



Length of pauses: 100, 80, 52, and 100 millisecc.

Fig. 4.—Oscillogram of vibrations of a pupa of *Aricia artaxerxes vandolica*. Upper line: one pulse-train, consisting of 5 pulses. Second line: First pulse, expanded in time 4x relative to first line. Lower 5 lines: Each pulse, expanded in time 20x relative to first line.

For comparison, a sonagram (Fig. 5) was made of a corresponding pulse-train in the same recording. There is a reasonable agreement between this "vibration sonagram" and the other sonagrams recorded with a microphone; it can thus be concluded that there have been no essential resonance phenomena from the recording vials.

Most of the vibrations registered in the recording (32 pulse-trains within 150 seconds) were like those in Fig. 4. At the beginning, however, when the pupa was evidently strongly irritated, it produced a more complicated vibration (oscillogram Fig. 6) several times. If comparing this observation with the top line of Fig. 4, it turns out that the latter has 5 pulses in 500 milise., but otherwise shows hardly any further oscillation (apart from the constant noise), while Fig. 6 has both a similar pulse-train with 6 (7) (slightly shorter) pulses within a little more than 250 millise., and also a series of rather regular fainter vibrations, about 25 in all in 500 millise. They start before the standard pulse-train, go on during it and continue for about 125 millise. afterwards.

Otherwise, no similar vibrations were registered in the experiments, neither by direct listening nor in the sonagrams, probably due to the extremely low sound pressure level. They may come from a different part of the pupa, possibly from the trace of the stridulatory organs which, as stated earlier, Downey (i.l.) found in the intersegmental cleft 6/7 in *A. artaxerxes vandolica* (and *A. agestis*).

Sounds provoked by external agitation (and other stimuli)

The sound produced is so faint as only to be audible if the pupa is placed in a small vial which is held close to the ear and shaken or tapped. The sound also is provoked if the pupa is touched or faintly tickled with a brush or a short hair (or by other insects and spiders).

The sounds from Lycaenid pupae have been variously described as "chirping," "creaking," "ticking," "buzzing," "humming," or "clicking" noises. To me the sound from *Aricia* pupae resembles the creaking of a door or the far distant chattering of a magpie. With a sensitive microphone at a distance of 1-2 cm it could easily be recorded.

Sound pressure of pupal sounds

An attempt was made to get a quantitative measure of the strength of the emitted sounds. Basically this was achieved by

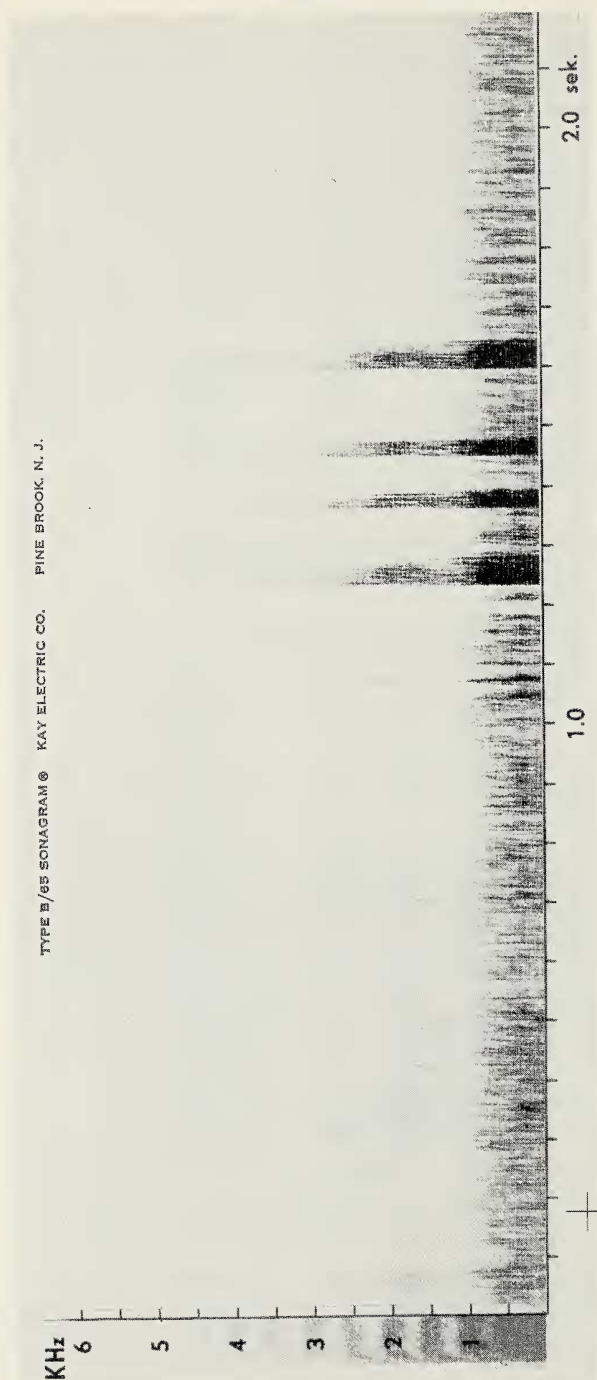


Fig. 5.—Sonagram from tape with vibrations of the same pupa as used for Fig. 4.

establishing the relationship between the sound pressure, acting on the microphone and the corresponding voltage at the output of the tape recorder during playback, using the same settings of the tape recorder controls as in the pupal recordings. This calibration was done against a Brüel & Kjaer 4135 microphone, 2619 preamplifier and a 2606 measuring amplifier.

Once this relationship was established, the recorded pupal sounds were displayed on a Hewlett-Packard 1201 A storage oscilloscope, where the peak voltage was measured. As the sounds were heavily overlaid with noise, correction was made for this, using parts of the record with no pupal sounds as a reference.

The estimate arrived at was 38 dB relative to 2×10^{-4} dyn/cm² at a distance of 1 cm. Several sources of errors are apparent in this procedure, above all the rather non-reproducible sound field in the recording jar, the effect of which is likely to cause an overestimate of the actual strength of the sounds. Ever so, the figure does show that these sounds are very faint indeed and only audible at extremely short range under quiet conditions.



Fig. 6—Oscillogram of vibrations of the same pupa as used for Figs. 4 and 5, showing two sets of vibrations, the minor ones consisting of pulses before, during and after the standard pulse-train. (Distorted, due to overload of tape.)

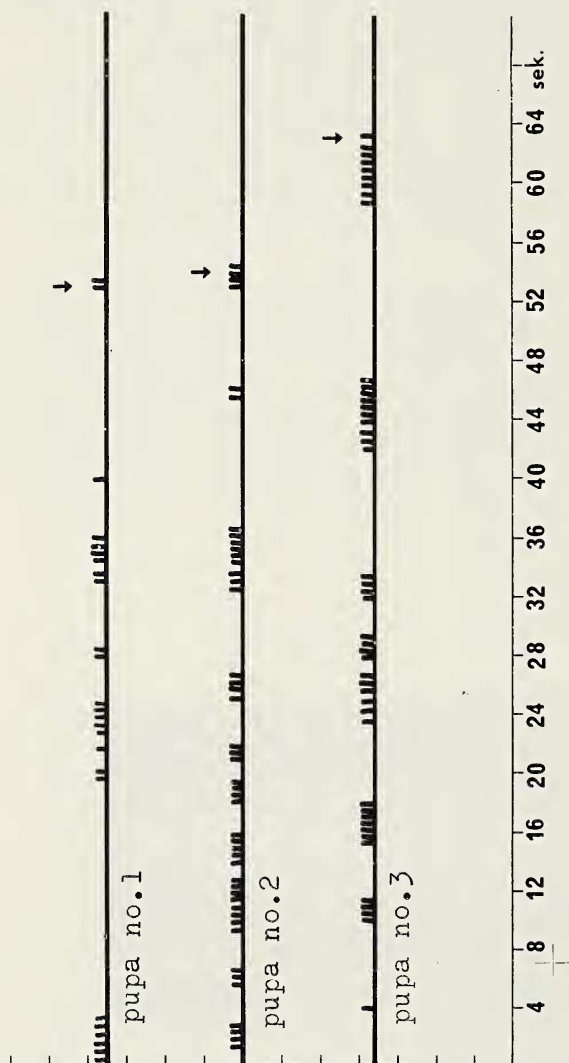


Fig. 7.—Spontaneous sounds, recorded by hand from a tape, from 3 pupae of *Aricia artaxerxes vandallia* during the last minute before emergence. At ↓ the pupal skin bursts.

Sounds and various circumstances

- a) Sound and pupal age. It was found that from the (3rd-) fourth day faint sounds could be made; during the last 10 days sound production was at its maximum; the sounds could be heard every day and remained constant as to both volume and character. Sounds could be emitted until the very moment the imago emerged (see later).
- b) Sound and individual, sex. Willingness to emit sounds varied from one pupa to another, but there was very little variation in the noise made by each individual pupa. The majority were willing enough throughout the 10 days, but some seemed to require some stimulus to start them off, while others made no sounds at all. If a pupa had been left in peace for many days it took a greater number of shaking movements to start off sound production. Excessive irritation could tire the pupae, making them silent for a time. The sounds from males and females were identical.
- c) Sound and temperature. Sound production was found to increase with a rise in the temperature.
- d) Sound and situation of the pupa. The situation of the pupae, be it inside its web within a withered leaf, or able to roll about freely, had no influence (excluding any surmise that sound-production might be connected with an attempt by the pupa to right itself).
- e) Sound, and noise, light, and smell. No sounds were produced while the pupae were exposed to loud noise, strong light or smell, (a piercing "cri-cri" sound from a toy cricket; a nitraphot lamp lighted for a few seconds at a distance of 15 cm; lactic acid or oil of cloves smeared on a glass rod near the pupa).

Spontaneous sounds

The pupae did, however, make spontaneous noises. From a tape recording from a vial containing 14 five-day old pupae (which had previously all produced audible sounds when shaken), placed in the dark, at normal room temperature and in absolute silence, it was found that in the course of 15 minutes 2 sounds were made at long intervals, each consisting of one pulse-train of normal type; this corresponds to an average of one sound per pupa every 105 mins. The frequency of sounds emitted was found to increase towards the end of the pupal stage,

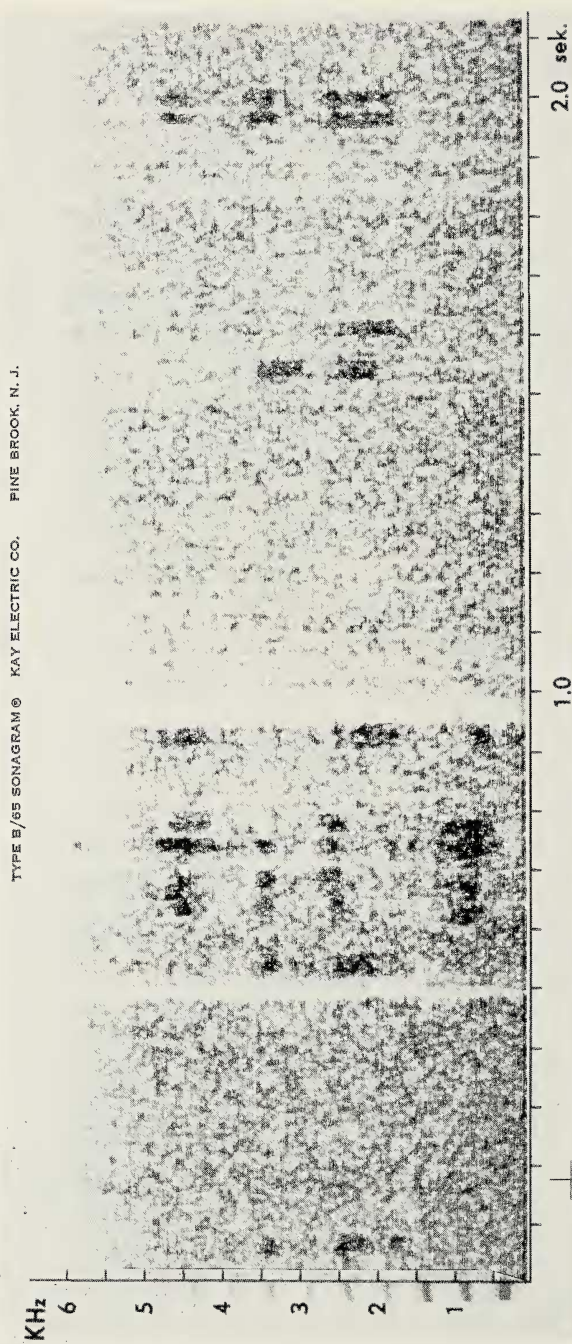


Fig. 8.—Sonagram of spontaneous sounds from an emerging *Aricia artaxerxes vandallia*, showing different pattern of pulses.

in the last hours being one sound per pupa every 3 minutes, and ending with a long sequence of sounds during the last minute before emergence (Fig. 7). This sequence started about a minute before the pupal skin bursts; at that moment some few last sounds could be recorded, and 15-30 seconds later the legs were out. The pulse-trains were formed in a different way than the normal ones (sonagram Fig. 8).

STRUCTURES AND SOUNDS IN *P. icarus*, *P. argus*, *C. argiolus* AND
Th. querqus

In principle, I found the same circumstances in the other four Lycaenid species as in the two *Ariciae*. However, while the reaction in *Ariciae*, *P. icarus* and *P. argus* (apart from the faint vibrations mentioned before) consisted of one kind of sound only—(4) 6-8 (10) pulses within 300-700 millisec.—I found both in *Celastrina argiolus* and *Thecla querqus* two sets of sounds of different character: Besides a sound similar to the creaking from *Aricia* pupae, here a faint buzzing at a quicker rhythm (about 14 per second) was heard, continuing for a long time. In a particularly willing *C. argiolus* it went on for hours even though the pupa was left quietly in peace. There was a great individual variation: Out of 18 *argiolus* pupae, 5 days old, only 4 emitted this sound, and only one of them continued—but then for several months—to react by this sound to any shaking action. The sonagram (Fig. 9) shows that these sounds have a narrower maximum intensity range, about 2.5-3 kHz.

FUNCTION OF SOUND

Introduction

The significance of these sounds for the Lycaenidae has been the subject of much speculation as it seems hardly credible that they have no function whatsoever, being identified as they are with a large natural family, distributed over the six major biographical regions of the globe.

The opinion has been voiced that the sounds are meaningless, being merely incidental phenomena accompanying the "gymnastic" movements of the pupae which are necessary for the internal transport of matter.

Two theories which may readily be dismissed concern the interpretation of the sounds as a signal to other individuals of the same species, in one case to larvae, as an instigation to congregation with a company of pupae (but the majority of

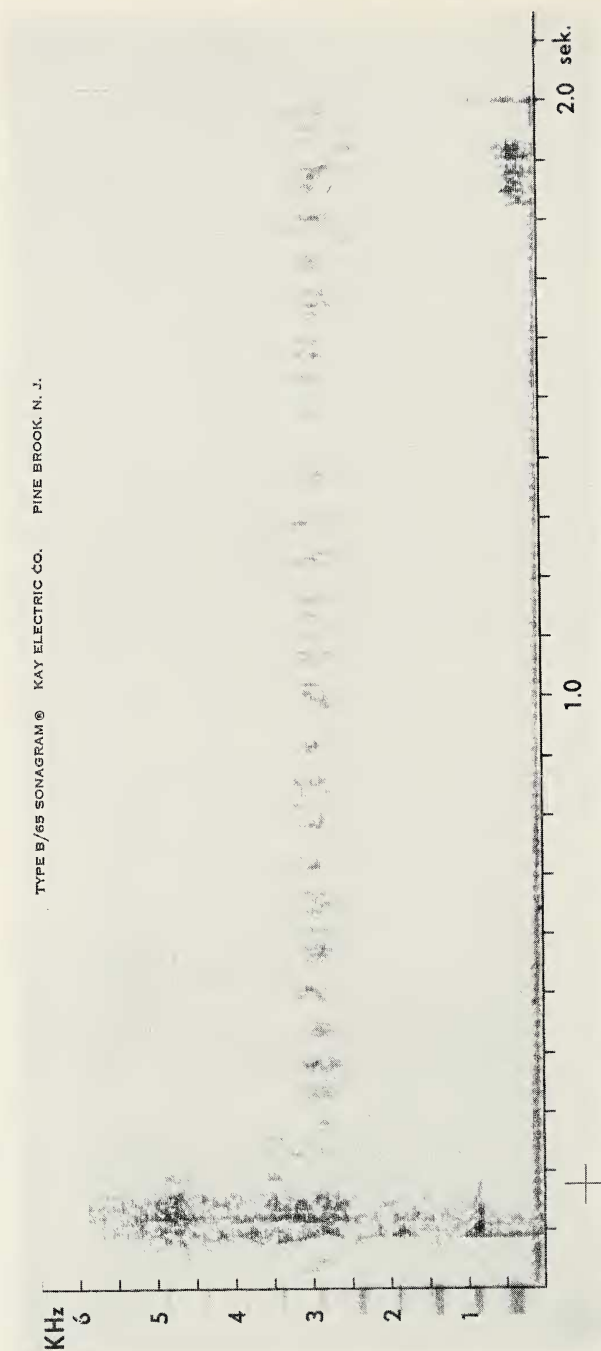


Fig. 9.—Sonagram of a pupa of *Celastrina argiolus*, showing perpetually whizzing sounds, with a maximum intensity range around 2.5-3 KHz.

Lycaenids are not gregarious) and in the other case to already emerged males, to cause them to remain in the proximity of a female pupa so as to achieve pairing as soon as the female has emerged (but this leaves unexplained the facts that some pupae make sounds months before they are mature, and that male pupae also produce sounds). In any case, butterflies have presumably no auditory sense, and such faint vibrations can certainly not be picked up at any distance by sense of touch amid the many ambient vibrations in nature.

The two theories which carry most weight are those which interpret the sounds as a defensive mechanism and those which associate them with myrmicophili.

A) The defensive mechanism theory has most adherents, although the objection has been raised that pupae are by no means so subject to predation as larvae, wherefore it should rather be the latter, which possessed the sound-production faculty; the fact that the sounds and vibrations (it must be vibrations, which are the important factor) are feeble can be no substantial objection, as a faint, unexpected buzzing can serve to scare off even humans, and a parasite or predator might well have its behaviour pattern interrupted by it.

Here I want to refer to the preceding experiment of placing a pick-up direct on the pupa; under natural conditions, the vigorous vibrations, intensified by dead leaves around the pupa, might no doubt have a deterrent effect. And the fact that the spontaneous sounds got more frequent just before the emergence may, of course, be an accidental attendant phenomenon caused by the animal's efforts to burst the pupa skin. However, it might very well be a preventive step against intruders at the coming act: This most critical period to the species and individual when the newly emerged imago always shows a nervous restlessness in its eagerness to find a resting-place where its wings can unfold and harden in peace.

B) The theory of myrmicophili (Thomann, 1901). Some of the Lycaenidae, presumably only a small minority (Malicky, 1969, 1970), live in a symbiotic relationship with ants, these protecting the larvae, feeding them, and transporting them, in some very few cases even into the ant-hill, while the larva, or in some cases even the pupa, in return yields the secretion of the exudatory gland. In such species as the last mentioned the emission of sounds (vibration) may readily be explained as a call to well-disposed ants. But it does not explain the fact that

those pupae which do not yield any secretion and that the species which have no symbiotic relationship with ants also produce such signals. The theory that it is a habit inherited from secretion-producing ancestors, and that larvae after tens of thousands of years by this means attempt to dupe ants into behaving beneficially and protectively towards them, seems hardly plausible.

With regard to the relationship of *A. agestis* and *A. artaxerxes* ssp. *vandalica* to ants, it should be mentioned that Harrison (1905) was the first to maintain that in nature, *agestis* larvae were always attended by ants. It has since been shown by Jarvis (1958-59) that ants were not so indispensable and that in artificial rearing they can be dispensed with entirely; that a simultaneous presence of *Lasius flavus* F. was purely coincidental; and that *Lasius niger* L. attacked the larva. Hoegh-Guldberg (1966) found *Formica pressilabris* Nyl., *exsecta* Nyl. and *pratensis* Retz. in the *artaxerxes* locality at Hirtshals, Jutland, Denmark, and in Jomfruland, Outer Telemark, Norway, and concluded that it must be these species which were involved in a symbiotic relationship if there was any. But both Jarvis and Hoegh-Guldberg have reared thousands of *Ariciae* without the presence of ants, and neither of them support the myrmicophilic theory.

EXPERIMENTS

In an attempt to throw light on the question, Dr. Bondesen and I enclosed, by turns, one or two specimens of presumed well-disposed ants, *Formica pressilabris* Nyl. and *F. exsecta* Nyl., with a pupa, but no sounds resulted, neither when they were in close proximity, nor—strangely enough—when they were actually touching the pupa. This was by no means the case when the same pupa was enclosed with the “hostile” *Lasius niger* L., or with *Leptothorax acervorum* F. or *Myrmica schenki* Emery. On the other hand, there was no reaction to *Formica truncorum* F. or *F. sanguinea* Latr. We did not register any stridulating sounds from the ants in these experiments. (We are indebted to Chr. Skoett, Horsens, for the procuring and determining these ants.)

These results tend to invalidate the theory of a connection between sound production and myrmicophili and speak in favour of a theory of sounds being a defensive mechanism, the more so since we were able to induce strong sounds by touching

the pupa with a brush or a human hair, or by enclosing it with a beetle (by turns *Pterostichus melanarius* Illig. (*vulgaris* L.), *Carabus granulatus* L. and *Coccinella 7-punctata* L. and with a common earwig, *Forficula auricularia* L.). In all these cases strong sounds were produced and invariably so immediately the strange insect touched the pupa. (A noteworthy phenomenon was observed when a small spider cautiously approached a pupa about 10 days old, at which age the dark eyes can be seen clearly through the pupal skin; when the spider was 1½ cm. away, two marked sounds were heard from the pupa.)

The experiments consequently have shown the reaction of Lycaenid pupae to some other animals. The experimental conditions oppositely did not permit observation of any reaction of insects or spiders to pupal sounds and vibrations—here is a field for future research.

FUNCTION OF SOUND

Overall result:

The pupal sounds in the Lycaenidae examined most likely can be interpreted as a defensive measure against other predating insects; however, it is hardly the faint oscillations in the air that deter, but rather vibrations that are transmitted through the underlay. To birds these phenomena probably may act as attraction, if they are perceived (cf. earthworms eaten by blackbirds); but this disadvantage has to be estimated against the larger danger from parasites.

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SUMMARY

1) Even though the ability to produce sounds in Lycaenid pupae has been known for 200 years, there seems to be a want of experimental work with live pupae.

2) In *Aricia artaxerxes* F. and *A. agestis* Schiff. was found a suggestion of stridulatory organs between segments 6 and 7 too.

3) Under different conditions, numerous experiments with tape recorder, sonograph, oscillograph, and video-tape have been carried through on pupae of 6 different Danish Lycaenid species, preferably *Aricia artaxerxes* which were considered particularly suited.

4) A movement of the intersegmental cleft 5/6 corresponded to the duration of a pulse in a pulse-train—there are consequently no extremely rapid movements.

5) The sonagram showed a series of sounds with a wide uniform frequency spectrum, ranging up to 5-6 kHz.

6) Besides, a continuous whizzing sound with a lower intensity range was found in *Celastrina argiolus* L. and *Thecla quercus* L.

7) The vibrations in *A. artaxerxes* were analyzed by oscillography, and such a similarity between the wave form of the single pulses in a pulse-train was found that they may be regarded as produced by a movement of the same teeth of the file against the same irregularities in the stridulating plate.

8) By an oscillograph analysis 2 sets of vibrations were found in *A. artaxerxes*, the usual ones, but also a series of fainter vibrations starting before the main pulse-train, going on during it, and ending afterwards. They may come from the intersegmental cleft 6/7.

9) The sound pressure of the usual signal was gauged to 38 dB relative to 2×10^{-4} dyn/cm².

10) The pupae emitted sounds from the time they have hardened, a few days old, and until the moment of emergence. There was an individual difference as to how easily sounds are provoked, they were alike in ♂ and ♀, independent of the situation of the pupa, increasing by raising temperature, not emitted by influence of noise, strong light, and pungent smells. They were only produced by shaking and touching.

11) Also spontaneous sounds occurred, increasing in number until the emergence, just before which there was a long series of sounds. The sonagram showing these emergence sounds differs from the normal sonagrams.

12) The theories on the function of the pupa sounds were examined. A series of experiments did not support the myrmicophilic theory; but the experiments will support the theory that the sounds—vibrations—serve as a defensive measure; and the emergence sounds might be a preventive arrangement in order to keep predators away before this most critical hour in the insect's life.

LITERATURE CITED

- BROUGHTON, W. B., 1963. In BUSNEL, R.-G.: Acoustic behaviour of animals, p. 3-24.
- DICKSON, C. G. C., 1952. The life history of *Phasis zeuco zeuco* L. *Trans. Roy. Soc. So. Africa*, 33(4):447-456.
- DOWNEY, John C., 1966. Sound production in pupae of Lycaenidae. *Jour. Lepid. Soc.*, vol. 20(3) p. 129-155.
- 1967. Sound-production in Netherland Lycaenidae. *Ent. Ber.*, 27, p. 153-157.
- HARRISON, J. W. H., 1905. Observations on *Polyommatus astrarche*. *Ent. Rec.* 17, p. 267.
- HINTON, H. E., 1948. Sound production in lepidopterous larvae. *Entomologist*, 81: 254-269.
- 1946. Concealed phases in the metamorphosis of insects. *Nature*, 157: 552-553.
- HOEGH-GULDBERG, OVE, 1966. North European Groups of *Aricia allous* G.-Hb. Their Variability and Relationship to *A. agestis* Schiff. *Aricia studies* 6 (*Natura Jutlandica* 13) Aarhus.
- JARVIS, F. V. L., 1958-59. Biological Notes on *Aricia agestis* (Schiff) in Britain, Part I-II-III. *Ent. Rec.* 70-71, p. 1-18, 169-178.
- MALICKY, H., 1969. Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera) *Tijdschrift voor Entomologie*, 112: 213-298.
- 1970. New aspects on the association between Lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). *Jour. Lepid. Soc.* 24: 190-202.
- PRELL, H., 1913. Über zirpende Schmetterlingspuppen. *Biol. Centralbl.* 33: 496-501.
- STRAWN, M. A., 1964. Sound production in pupae of the butterfly family Lycaenidae. Unpublished Masters Thesis, Southern Illinois University.
- THOMANN, H., 1901. Schmetterlinge und Ameisen. Beobachtungen über eine Symbiose zwischen *Lycaena argus* L. und *Formica cinerea* Mayr. *Jahresber. Nat. Ges. Graub.* 44: 1-40.